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Long term drivers of change in *Polylepis* woodland distribution in the central Andes

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Abstract

Question: Is the modern patchy distribution of highly biodiverse *Polylepis* woodlands a consequence of human activity or, natural fluctuations in environmental conditions? What are the consequences of changing climate for the tree genus *Polylepis*?

Location: High central tropical Andes.

Methods: We characterise the ecological baseline conditions for *Polylepis* woodlands over the last ca. 370,000 years through: i) examination of fossil pollen records (Salar de Uyuni and Lake Titicaca) and, ii) a review of autecological information concerning *Polylepis*.

Results: Fossil pollen data reveal fluctuations in the abundance (c. 0-34%) of *Polylepis* pollen prior to the arrival of humans in South America (>12,000 years ago). Indicating that *Polylepis* did not form permanent continuous woodland prior to the arrival of humans and that climatic factors can drive rapid vegetation change. Autecological assessment of *Polylepis* reveals: i) negative moisture balance, ii) fire, iii) waterlogging, and iv) cloud cover to be critical to determining the niche space available for *Polylepis*.

Conclusions: *Polylepis* niche space in the central Andes was at a maximum during warm and wet conditions in the past, but might be at a minimum during the warmer and drier-than-modern conditions predicted for later this century. The sensitivity to past global climate change emphasises the need for conservation planners to consider model predictions of a warmer central Andes in the coming decades when developing planting schemes. Natural fluctuations in woodland abundance suggest the most effective way for conservation efforts to

‘mimic’ the natural baseline would be to develop a reproductively connected patchwork of communities.

Words 249 /250

Key-words: Andes; biodiversity; Bolivia; charcoal; climate change; moisture balance; Peru; pollen; *Polylepis*; seasonality; temperature.

Abbreviations: kyr BP = thousands of years before present (^{14}C ages calibrated where appropriate); LGM = Last Glacial Maximum; MIS = Marine Isotope Stage; masl = meters above sea level; UV-B = Ultra Violet-B; PAR = Photosynthetically Active Radiation.

Nomenclatural reference: Judd et al. (1999)

1 Introduction

2
3 Ecological data sets from around the globe have revealed the variable, but measurable,
4 response of taxa to current climate change (Parmesan 2007; Pounds et al. 2006).
5 Consequently, it is now recognized that effective conservation and development of
6 ecosystems needs to be coupled with a thorough understanding of ecosystem function
7 (Pressey et al. 2007; Soulé & Wilcox 1980). Ecological observations and historical records
8 permit us to view ecological change through the past tens to hundreds of years, e.g.
9 environmental inventories (Diaz & Markgraf 1992) or phenological observations (Schnelle
10 1955). However, to examine ecological change on longer time frames it is necessary to
11 explore the palaeoecological record, e.g. fossil pollen, charcoal, seeds or fruit (Godwin 1956).
12 Palaeoecological records can extend our understanding of past environmental change both
13 temporally and spatially beyond the presence, or even existence, of humans, allowing times
14 and areas without a long written human history to be examined. Fossil records can inform
15 conservation and development strategy formulation by: i) providing baseline indices of
16 biodiversity, and ii) quantifying ecological response to global climate change (e.g. Willis et
17 al. 2007; Birks & Birks 1980).

18 The vegetation of the high central Andes is known as ‘Puna’ and is dominated by cold
19 and dry adapted shrubs (predominantly Asteraceae and Brassicaceae species) and grasses
20 (Poaceae). Within the grassland matrix woodlands dominated by the treelet genus *Polylepis*
21 are enclaves of high biodiversity that have attracted the attention of conservationists and
22 ecologists. Long-term persistence of such woodlands in the Andean landscape is suggested by
23 the number of habitat specialists and endemic species that they support (Cahill & Matthysen
24 2007; Fjeldså & Kessler 1996).

It has been suggest that *Polylepis* woodlands are the ‘climax’, or mature landscape vegetation type, for a considerably larger area than they presently occupy. Indeed, the current patchy distribution pattern of *Polylepis* woodland has been widely attributed to human activity (Kessler 2002). Ellenberg (1958) first suggested that a long history of poor human resource management in the landscape could have resulted in the fragmentation of more extensive woodland cover, i.e. the destruction of woodlands for building material, fuel wood and charcoal. The value of the *Polylepis* timber within this landscape is clear and there is increasing evidence of the detrimental effect of modern human activity on sustaining, and re-establishing, *Polylepis* through grazing (Teich et al. 2005), soil degradation (Renison et al. 2005; Renison et al. 2004) and fire (Renison et al. 2002). Additionally, evidence from soil charcoal indicates that fire has played an important role in determining woodland distribution in the Andes on longer timescales (1000s of years) (di Pasquale et al. 2008); although the origin of these fires (natural or human) remains ambiguous. Despite the observed detrimental impact of humans activity upon woodland cover assertions that *Polylepis* was once naturally much more widespread than today are largely speculative, relying on known aspects of its fundamental niche to infer past abundance and distribution (Cierjacks et al. 2007; Kessler 2002).

Using temperature and precipitation as niche-defining variables, the distribution of *Polylepis* species should expand across a wide range of settings up to c. 4200 masl (metres above sea level) in the central eastern humid Andes, and possibly as high as c. 5000 masl in the central western cordillera (Kessler 2002). Local modifications to this distribution would occur as a result of poor tolerance to waterlogging (flat valley bottoms), salty condition (absence from salars), aridity (required >100 mm precipitation per year) and extremely humid conditions (Fjeldså & Kessler 1996). Climate niche models and reconstructions based upon present day distributions estimate *Polylepis* cover to have been reduced by as much as 98%

(Fjelds  & Kessler 1996). Reforestation projects in the Puna grasslands of Peru and Bolivia using native species are being encouraged by conservation organizations that sense the possibility of a win-win between habitat restoration and carbon sequestration (Fehse et al. 2002). Most of these programs emphasize the planting of *Polylepis* because of its ecological tolerance to high elevations and its presumed former range. In the absence of confirmatory records, these plantings are restoration to an assumed baseline (*sensu* Pauly 1995) rather than to one that is known.

Fossil pollen records from the central Andes demonstrate fluctuations in *Polylepis* abundance since the Last Glacial Maximum (LGM; c. 21 kyr BP [thousand years before present; ¹⁴C calibrated where appropriate]) e.g. Paduano et al. (2003). However, the presence of humans in the landscape for much of this time means that the relative effect of factors driving these changes (human vs. climate) remains unclear. The only other record of vegetation change from the Andes to extend beyond the LGM comes from the Sabana de Bogotá (Colombia) (Hooghiemstra 1984). Through the last glacial-interglacial cycle fossil pollen from Lake Fuquene (5° 27' N, 73° 46' W; 2580 masl) shows variation in abundance of *Polylepis* (van der Hammen & Hooghiemstra 2003).

In this paper we integrate the first southern hemisphere fossil record of *Polylepis* type pollen covering multiple glacial-interglacial cycles with a review of existing *Polylepis* autecological data. The combination of palaeoecological evidence from prior to human arrival in South America and ecological data allow us to quantify the response of *Polylepis* to past global climate change and to provide insights on the temporal and spatial permanence of *Polylepis* woodlands.

Methods

The genus *Polylepis* Ruiz & Pav. is a member of the Sanguisorbeae tribe of the Rosoideae subfamily of Rosaceae (Simpson 1986). Twenty-eight species of *Polylepis* have been recognised (Schmidt-Lebuhn et al. 2006). The central Andes (Bolivia/Peru) are an ideal location to examine both the environmental history and autecology of *Polylepis* because fossil records are available (Fig. 1) and the region is the centre of diversity for the genus (Navarro et al. 2005). In the central Andes, 15 species of *Polylepis* are present which together cover an altitudinal range of 3400 m (from 1800 to 5200 masl; Fig. 2a-b) (Fjelds  & Kessler 1996). This altitudinal and latitudinal range defines the extent of the environmental envelope that can be examined through the investigation of this genus from a palaeoecological perspective because it is impossible to differentiate *Polylepis* pollen below genus level.

Palaeoenvironmental records

Polylepis has inconspicuous wind pollinated flowers (Simpson 1986) but is regarded as a poor disperser of pollen (generally <1 km) (Kuentz et al. 2007). However, evidence from genetic studies suggests that long distance dispersal of *Polylepis* pollen makes a significant contribution to the genetic mixing of this genus (Schmidt-Lebuhn et al. 2007) and some species have been found to disperse over >30 km (Seltmann et al. 2009). Pollen grains found in lake sediments are therefore likely to represent a regional vegetation signal. The fossil pollen records from Salar de Uyuni (20 S 68 W, 3653 masl) and Lake Titicaca (16 S 69 W, 3810 masl; Hui naimarca and Lago Grande) are unrivalled in length in the southern hemisphere Andes and therefore represent the best possible opportunity to investigate changes in *Polylepis* woodland extent over glacial-interglacial cycles (Fig. 3a-c); i) Salar de Uyuni c. 18-108 kyr BP (Chepstow-Lusty et al. 2005; Fritz et al. 2004), ii) Hui naimarca c. 0-230 kyr BP (Gosling et al. 2008), and iii) Lago Grande c. 0-370 kyr BP (Hanselman et al. in review; Hanselman 2007). Today different *Polylepis* species are present in woodland patches within a

few kilometres of Lake Titicaca (*P. besseri* and *P. racemosa*) and the Salar de Uyuni (*P. tomentella* and *P. tarapacana*) (Fjelds  & Kessler 1996; Fig. 1).

Identification of the genus *Polylepis* in the fossil pollen record is problematic due to its morphological similarity with herbaceous *Acaena* (Smit 1978); a genetically closely related genus within the Rosaceae (Schmidt-Lebuhn et al. 2006). However, we are confident that it is most likely that majority of the *Polylepis* type pollen grains captured in these lake systems represent woodland because of: i) the geographical restriction of *Acaena* (Kuentz et al. 2007; Chepstow-Lusty et al. 2005), and ii) the preference of *Acaena* for recently burned Puna, i.e. it is largely absent from established Puna (M.B. Bush pers. obs.). Due to this uncertainty in identification we have designated this taxa “*Polylepis* type”.

Fossil pollen records from Salar de Uyuni and Lake Titicaca were prepared and analysed using standard procedures (Faegri & Iversen 1989). Samples were examined under light microscopes at x400 and x1000 magnification. Identification of pollen grains was achieved using the pollen reference material at Florida Institute of Technology, the “Neotropical Pollen Database” (Bush & Weng 2007) and pollen atlases (Faegri & Iversen 1989; Hooghiemstra 1984). Fossil charcoal material from Lago Grande was prepared using standard methodologies (Whitlock & Larsen 2001), identified and digitally photographed using a binocular microscope (x20 magnification) and area calculations determined by interrogating the digital images with Image J software (Rasband 2008). Diagrams were generated using C2 software (Juggins 2005). Chronologies for the Salar de Uyuni and Lago Grande records are as published, the Hui naimarca chronology modified slightly and extended from Gosling et al. (2008) in light of new tephra chronology data (Tomos 2008) (Fig. S1).

Results

1 **Past changes in *Polylepis* abundance**

2 Fossil pollen analysis of lake sediments from Salar Uyuni, Huiñaimarca and Lago
 3 Grande reveal non-tree pollen (mainly grasses) dominate the signal (mean 86%) throughout;
 4 however underlying this, wide fluctuations in the proportional abundance of *Polylepis* type
 5 pollen are evident (ca. 0-34%). The Salar de Uyuni record is intermittent from 18 to 108 kyr
 6 BP (fluctuating between a salt pan and lake) but within the lake sediments, where pollen is
 7 preserved, *Polylepis* type comprises 0-26% (Fig. 3a). The Huiñaimarca pollen record covers
 8 c. 230 kyr BP during which *Polylepis* type varies 0-26% (Fig. 3b) and the Lago Grande
 9 record, which spans the last c. 370 kyr BP, contains *Polylepis* type between 0-34% (Fig. 3c).
 10 The maximum proportion of *Polylepis* pollen recorded at Lake Titicaca during the Holocene
 11 is c. 20% (Paduano et al. 2003). *Polylepis* pollen reaches >20% ten times in the three records
 12 presented here at: c. 322, 300, 232, 210, 162, 139, 115, 94, 44 and 21 kyr BP (Fig. 3a-c).
 13 Variations in the proportions of other tree taxa do not follow the same pattern as *Polylepis*
 14 type; Pearsons correlation coefficient *Polylepis* vs. other arboreal pollen: Lago Grande $r = -$
 15 0.016 ($n = 516$), Huiñaimarca $r = -0.050$ ($n = 181$), Salar de Uyuni $= -0.130$ ($n = 129$) (SPSS
 16 v. 14.0).

18 **Fire history**

19 In the Lago Grande record, fossil charcoal was found in 48% of all samples investigated
 20 and the four highest concentrations were found at: 326 kyr BP (4.3 mm/cm^3), 212 kyr BP (1.8
 21 mm/cm^3), 138 kyr BP (2.9 mm/cm^3) and 7 kyr BP (2.1 mm/cm^3) (Fig. 3d). There is a weak
 22 positive correlation between charcoal concentration and *Polylepis* pollen (Pearsons
 23 correlation coefficient for interpolated data: $r = 0.139$ significant at 0.01 level (two tailed)
 24 (SPSS v.14.0)). Elevated concentration of charcoal in the fossil record occurs in association

with increased proportion of *Polylepis* pollen and warm, interglacial or transitional, conditions.

Discussion

Autecology of *Polylepis*

Moisture and temperature (insolation) have been identified as controlling factors on *Polylepis* distribution in the Andes (e.g. Rada et al. 2001; Rada et al. 1996; Fig. 2b). However, the variation of insolation and moisture in the Andes is modified by multiple factors, principally: altitude, latitude and topography (slope angle, aspect). The upper limit on moisture is determined by waterlogging which is principally a function of precipitation and topography, i.e. *Polylepis* is often excluded from poorly- drained, flat- bottomed valleys (Kessler 2002). The lower moisture limit (aridity) for *Polylepis* in the central Andes is c. 100-200 mm/yr and it is excluded from soils with elevated salinity (Fjeldså & Kessler 1996). In regions where precipitation is close to the 100-200 mm/yr minimum threshold, radial tree growth is positively correlated with precipitation and negatively with insolation (due to the detrimental impact of increased insolation upon moisture availability) (Morales et al. 2004). *Polylepis* has been observed to switch energy away from sexual to asexual reproduction when subject to low moisture availability (Cierjacks et al. 2007) and low temperatures (Hertel & Wesche 2008), allowing the taxon to persist in marginal environments through unfavourable conditions. Where precipitation is >200 mm/yr insolation has been established as a key controlling factor in both *Polylepis* woodland location (Braun 1997) and tree growth (Kessler et al. 2007; Hoch & Körner 2005).

Fire frequency and intensity are related to aridity (i.e. precipitation), fuel load (i.e. is there something to burn), and ignition source. Today, fires occur principally as a result of

human activity but can probably also be started naturally by lightening strikes. Fire reduces *Polylepis* adult and inhibits regeneration (Cierjacks et al. 2008; Renison et al. 2002).

Moisture from clouds permits *Polylepis* to survive in areas of otherwise low moisture availability. However, high moisture availability due to persistent cloud cover, such as on the eastern Andean flank, allows competition from other, less drought tolerant, taxa leading to more mixed woodlands. Therefore the lower elevation limit of *Polylepis* is controlled by competition which is modified by the formation of cloud base.

High doses of insolation, particularly UV-B (Ultra Violet-B) and PAR (Photosynthetically Active Radiation) components, can have a detrimental impact upon the photosynthetic success of plants (Lavola et al. 1997). There is a concomitant increase in UV-B and PAR radiation with elevation in the Andes due to reduced absorption from the atmosphere and cloud cover. *Polylepis tarapacana* has been shown to have developed adaptations to cope with the elevated radiation at high altitude (Gonzalez et al. 2007). Therefore, changes in factors that modulate the amount of radiation reaching the vegetation in the high Andes, such as cloud cover, would be anticipated to have an impact on *Polylepis* and possibly the relative success of different *Polylepis* species.

Polylepis in the central Andes has also been identified as sensitive to climate at various stages of its life cycle: i) seed germination is aided by moist soils and protection from winds (Cohen et al. 2005), ii) seeds falling within woodland are more likely to germinate and the seedlings produced are more likely to be more successful when compared with those falling outside woodland (Cierjacks et al. 2007), iii) seeds produced by trees in ‘well preserved’ habitat are likely to produce seedlings that do better than those from ‘degraded’ habitat (Renison et al. 2005), and iv) lower temperatures can result in a switch from sexual to asexual reproduction (root suckers) (Hertel & Wesche 2008). These traits suggest that any climate change effect of on *Polylepis* success could result in rapid change in the amount of pollen

being recorded in the fossil record. More favourable conditions would facilitate a positive feedback by allowing woodlands to flourish, therefore produce better seeds and modify the local microclimate, leading to higher numbers of seedlings germinating and being successful and so expanding the woodland and producing more pollen. Whereas less favourable conditions would lead to a rapid decline in the amount of woodland being recorded in the fossil pollen record due to a switch away from sexual reproduction, i.e. no pollen being produced.

Past climate change and *Polylepis* abundance

Today the altitudinal range of *Polylepis* is c. 1800 to 5200 masl. Warming since the last glacial period is thought to have allowed taxa to move upslope by c. 1500 m altitude (Bush et al. 2004). Lake Titicaca is located at 3810 masl and therefore is theoretically within the ‘natural’ range of *Polylepis* continually through glacial-interglacial climate fluctuations. Consequently, if the patchy distribution of *Polylepis* in the landscape today is purely a product of human activity breaking up a continuous woodland ecosystem across the Andes up to c. 4800 masl, we would anticipate that prior to human arrival (>12,000 years) *Polylepis* would be abundant and ever present in the fossil pollen record. However, Hanselman et al. (in review) revealed *Polylepis* pollen abundance in Lake Titicaca fluctuated between c. 0 and 34% over the last four glacial-interglacial cycles (Fig. 3c). These data clearly demonstrate natural factors modulated the distribution, abundance and ability of *Polylepis* to produce pollen on these time-scales. This conclusion is supported by the similar magnitude changes in *Polylepis* evident in the fossil pollen record from the northern hemisphere tropical Andes (Lake Fuquene) over the last c. 124 kyr (van der Hammen & Hooghiemstra 2003).

Comparison of the fossil pollen records of *Polylepis* type pollen reveal broad scale coherent change (Fig. 3a-c). Transitional periods between global glacial and interglacial

climate conditions equate to periods of maximum proportion of *Polylepis* type pollen while aridity leads to the lowest abundances. However, shorter term (millennial) scale fluctuations between records do not appear to be synchronous between the central Andean study sites (Fig. 3a-c) or with those of the northern hemisphere record from Lake Fuquene (van der Hammen & Hooghiemstra 2003). The absence of fine scale correlation could be a product of: i) uncertainties in the chronologies, ii) differences or fluctuations in basin sizes, or iii) a product of an intrinsic landscape variability in the distribution of *Polylepis* through time, i.e. forming only in patches where microclimate permits, as opposed to a continuous woodland belt.

The presence of charcoal throughout the Lago Grande record reveals for the first time that fire is a natural component of Andean ecosystems through glacial-interglacial cycles; albeit at an intermittent and low level for much of this time. The major peaks in charcoal occur in association with warm, interglacial, conditions and/or high proportions of *Polylepis* pollen. This indicates that under warm and wet conditions the landscape can carry fire when there is sufficient fuel load. Under warm or cold and dry conditions burning occurs but peaks are smaller due to the reduced fuel load, under cold and wet conditions there is limited burning probably due to low fuel load and difficulty in ignition.

Fire is thought to be a key mechanism for maintaining woodland patches today (Renison et al. 2002) and during the Holocene (di Pasquale et al. 2008). Given that fire has been present in the Andean landscape for large periods of the last 370 kyr (Fig. 3d) it therefore seems likely that: i) this process will have maintained the patchiness of *Polylepis* woodland through this period and, ii) might be a partial explanation as to why *Polylepis* never dominates the pollen record (limited to maximum c. 20% peaks).

Drivers of past changes in *Polylepis* distribution

1 The proportions of *Polylepis* pollen found within the Salar de Uyuni and Lake Titicaca
 2 cores combined with our knowledge of past global climate change and autecological
 3 assessment allow us to predict change in distribution under a range of climate change
 4 scenarios relative to modern conditions: i) warmer and wetter (Fig. 2c), ii) colder and wetter
 5 (Fig. 2d), iii) colder and drier (Fig. 2e), and iv) warmer and drier (Fig. 2f). Inferences
 6 regarding past climate conditions are drawn from records of global (Jouzel et al. 2007;
 7 Martinson et al. 1987) and regional (Hanselman et al. in review; Paduano et al. 2003) climate
 8 change.

9 Warmer and wetter than modern conditions are thought to have occurred in the high
 10 Andes during the transitions into, and out of, the previous interglacial. During these times
 11 *Polylepis* pollen was at its maximum percentage in the Lake Titicaca records (Fig. 3b-c) while
 12 Salar de Uyuni remained a salt pan (negative moisture balance). Warmer and wetter
 13 conditions can be invoked for the central Andes by elevating moisture transport across the
 14 Amazon basin. If cloud base were to raise *Polylepis* would be excluded from the base of its
 15 elevational range (either by competition or waterlogging). At the same time, increased
 16 moisture transport to higher elevations and reduced ice cover would have allowed the genus
 17 to expand from valley patches into areas that are currently too arid to support it. Given the
 18 modern geographical distribution it seems likely that *P. besseri* and *P. tarapacana* would be
 19 the most likely to benefit around Lake Titicaca and on the eastern Andean flank. The most
 20 recent peak in *Polylepis* occurred during the transition into the current interglacial (equivalent
 21 Marine Isotope Stage [MIS] 1). Starting from wet, cool condition of the LGM the climate
 22 gradually warmed and became drier during deglaciation, following the pattern described by
 23 Paduano et al. (2003). Within this transitional period *Polylepis* reached up to 21% of the
 24 pollen sum, indicating an extensive presence around Lake Titicaca (Fig. 3c).

Colder and wetter than modern conditions occurred in the central Andes during the end of the Pleistocene glaciation (LGM). At this time, ice sheets near Lake Titicaca probably descended to between 3400 and 4300 masl, depending on local moisture availability (Smith et al. 2008). Iced conditions would have excluded *Polylepis* from high altitudes but melt supplied water to lower elevations, which, coupled with lower evaporation and probably increased precipitation (Baker et al. 2001), resulted in the formation of lakes at Uyuni. Concomitantly reduced temperatures are likely to have: i) lowered cloud base allowing *Polylepis* to flourish at lower elevations, but ii) increased the probability of poor growing conditions due to waterlogging in some areas. During this time there is no record of *Polylepis* growing around Lake Titicaca. The rapid increase in *Polylepis* type pollen following cold/wet conditions suggests that *Polylepis* populations (probably *P. besseri* and *P. racemosa* around Titicaca) persisted in nearby isolated valley patches where microclimates were tolerable and were able to quickly respond to more favourable conditions.

Colder and drier- than- modern conditions occurred around Lake Titicaca during previous stadials (e.g. MIS 3) and resulted in an absence, or near absence, of *Polylepis* (probably *P. besseri* and *P. racemosa*) in the fossil pollen records at Lake Titicaca (Fig. 3b-c). Low percentages in the fossil pollen data indicate that at high elevations *Polylepis* was probably restricted to isolated patches in favourable valley microclimates. Consideration of the autecology suggests that the distribution should expand down slope and on the eastern Andean flank as there would have been a concomitant reduction in cloud cover and waterlogging. The persistence of *Polylepis* (probably *P. tarapacana*) in the landscape below the elevation of Lake Titicaca is supported by the rise in *Polylepis* during MIS 3 at Uyuni which is c. 150 m lower in elevation than Titicaca (Fig. 3a). At Uyuni moisture from melt water created a lake and so allowed the accumulation of lake sediments which preserved a record of the presence of *Polylepis* in the regional landscape. It is worth noting that the

1 absence of suitable sediments for preserving pollen at Uyuni (i.e. salt deposits) does not mean
 2 that *Polylepis* was absent from the regional vegetation, only that there is an absence of any
 3 record. Indeed the high percentage of *Polylepis* recorded as soon as lake sediments were
 4 preserved suggests that the taxon persisted around Uyuni much of the time it was a salt pan,
 5 as it does today.

6 Warmer and drier- than- modern conditions occurred during the peaks of preceding
 7 interglacial periods (e.g. MIS 5.5, Hanselman et al. (2005); Fig. 3e) these conditions resulted
 8 in a decrease in the proportion of *Polylepis* within the Lake Titicaca sediments; too dry for *P.*
 9 *besseri* and *P. racemosa*, and too warm for *P. tarapacana*. In addition, cloud base will
 10 probably have remained relatively high because warmth would have tended to cause ground
 11 level cloud to form higher on a hillside than cold conditions. We infer that under warm dry
 12 conditions the niche space available for *Polylepis* would be restricted by the upward
 13 migration of cloudbase at the foot of its range and by aridity at the top of its range. *Polylepis*
 14 probably persisted in isolated patches within favourable microclimates within inter-Andean
 15 valleys and on the eastern Andean flank.

16 The topographic form of the Andes, with the largest proportion of land at c. 3600-4000
 17 masl, means that it can be anticipated that the maximum abundance of Andean woodlands
 18 will occur when there are favourable climatic conditions at these elevations. Salar de Uyuni
 19 and Lake Titicaca (3653 and 3810 masl) both fall within this range so it can be assumed that
 20 peaks in *Polylepis* percentage pollen recorded at these locations equate to maximum
 21 abundances within the central Andes generally. Conversely unfavourable conditions for these
 22 elevations will have a disproportionately large detrimental impact.

23 Although containing elements of uncertainty model predictions of future climate in the
 24 central Andes suggest that by the period 2020-2029 temperature will be between 0.5 and 1°C
 25 warmer annually and that there will be a decrease in wet season (June-July-August)

precipitation (IPCC 2007). Our findings for reduced *Polylepis* niche space during warmer and drier than modern conditions (Fig. 2f) conform to predictions that high Andean woodlands could be particularly vulnerable to predicted future climate change (Bush 2002; Malcolm et al. 2006).

Conclusions and implications

The combination of ecological and palaeoecological data has allowed us to quantify a number of likely ecological responses of *Polylepis* woodlands in the central Andes to global climate change:

- Adequate insolation and >200 mm/yr precipitation (without waterlogging) is optimal for the flowering of *Polylepis*.
- The baseline ‘natural’ abundance of *Polylepis* fluctuated between near absence and ten times the present level over the last c. 370 kyr; indicating significant natural changes in habitat and carbon storage.
- Fire is a natural feature of ecosystems in the high Andes under a variety of past climate conditions during the last c. 370 kyr.
- *Polylepis* did not form permanent continuous woodland in the high central Andes prior to the arrival of human, because during the last 370 kyr: i) *Polylepis* type pollen at no point dominates the fossil record, ii) discrepancies in variance between the fossil pollen records at millennial and sub-millennial timescales suggest non-uniform expansion and contraction at a landscape scale, and iii) the persistent presence of fire provides a mechanism for maintain patches through the whole period.

- Drier than modern conditions during previous interglacial periods reduced the abundance of *Polylepis* and consequently restricted the establishment of woodland communities.
- The maximum abundance of *Polylepis* is coincident with times of warmer and wetter conditions while warmer and drier conditions minimise optimum habitat.
- The climatically and environmentally sensitive nature of *Polylepis*, and the associated woodland ecosystem, in the Andean landscape may indicate a mechanism for placing selective pressure upon species.

The high central Andean woodlands are extremely vulnerable to predicted future global climate change over the next 20-30 years (Hanselman et al. in review). The slow growth rate of *Polylepis* (30 years to reach maturity) means that any planting schemes (for biodiversity preservation, carbon sequestration or the development of natural resources) should consider the likely negative effect of predicted warming especially on populations planted in regions close to the 100-200 mm/yr aridity threshold. Conservation of this biodiverse ecosystem would therefore be best served by judicious planting taking into consideration microclimatic, soil and topographic variations in addition to insolation and moisture availability. The natural base line for *Polylepis* in the central Andes has not, during the last c. 370,000 years, been permanent continuous woodland. Therefore, planting schemes which seek to establish a patchwork of reproductively connected communities are likely to be the best ‘mimic’ of the natural distribution and have the potential to vastly increase the abundance of woodland in the landscape.

Acknowledgements

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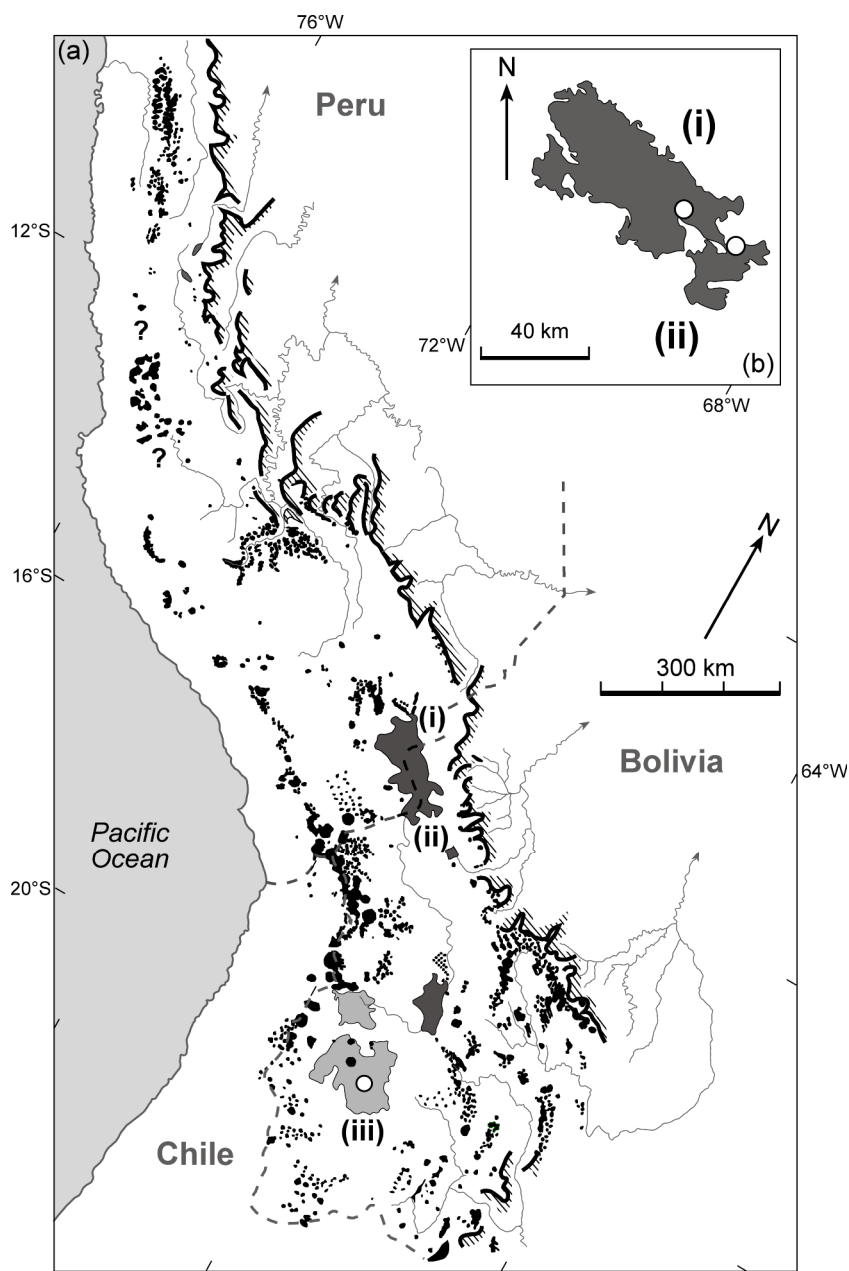
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conservation and the relevance of long-term ecological studies. *Philosophical
Transactions of the Royal Society B: Biological Sciences* 362: 175-186. **Figure
captions**

Fig. 1. a) Central Andean woodlands today and location of Uyuni core site. b) Lake Titicaca
core sites. Symbols: Black patches = high Andean *Polylepis* woodlands, black line with
diagonal hash = upper limit of continuous humid forest (potentially containing some
Polylepis), mid-grey = water bodies, light-grey = salt pans, dashed line = political boundary
(figure redrawn and modified from Fig. 4-4, p. 30, in Fjelds  & Kessler 1996). Black circles
with white fill = core sites, places marked with numerals: i) Lago Grande (Lake Titicaca), ii)
Hui naimaca (Lake Titicaca), and iii) Salar Uyuni.

Fig. 2. Distributional and conceptual model of environmental pressures on *Polylepis*
woodland in the central Andes. Under modern climate conditions: a) natural distribution of
Polylepis in Bolivia today redrawn from Fjelds  & Kessler (1996, figure 6-5, p. 72), b)
conceptual model of factors determining modern distribution of *Polylepis* in Bolivia today
(modified from Fjelds  & Kessler, 1996). Changes inferred to *Polylepis* distribution as a
consequence of different past climate conditions: c) warmer/wetter conditions, d)
colder/wetter conditions, e) colder/drier conditions, and f) warmer/drier conditions. Black
spots = *Polylepis* realised niche, dark grey shading = *Polylepis* potential niche, light grey
shading = Altiplano, T in yellow circle = Lake Titicaca, U in yellow circle = Salar Uyuni,
diagonal fill = ice sheets.

Fig. 3. Palaeoenvironmental records. Fossil pollen percentages for *Polylepis*, other arboreal pollen (other AB) and non-arboreal pollen (NAB) in sediment cores recovered from: a) Salar de Uyuni (20°S 68°W, 3653 masl; Chepstow-Lusty et al. 2005; Fritz et al. 2004), b) Huiñaimarca (16°S 68°W, 3810 masl; Gosling et al. 2008; Tomos 2007) and c) Lago Grande (16°S 69°W, 3810 masl; Hanselman et al., in review). See Table S1 for pollen taxa classified as ‘other AB’ and ‘NAB’. d) Charcoal concentration in Lago Grande (x indicates sample point); and e) °C variation relative to modern EPICA (Jouzel et al. 2007). MIS = Marine Isotope Stages after Martinson et al. (1987).

1 Figure 1



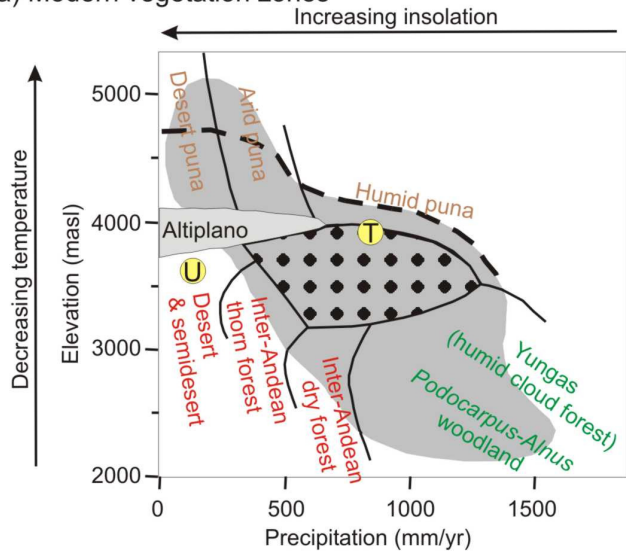
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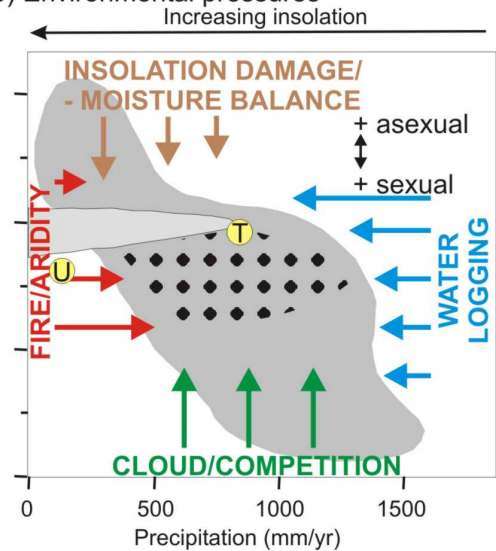
1 Figure 2

Modern

a) Modern vegetation zones

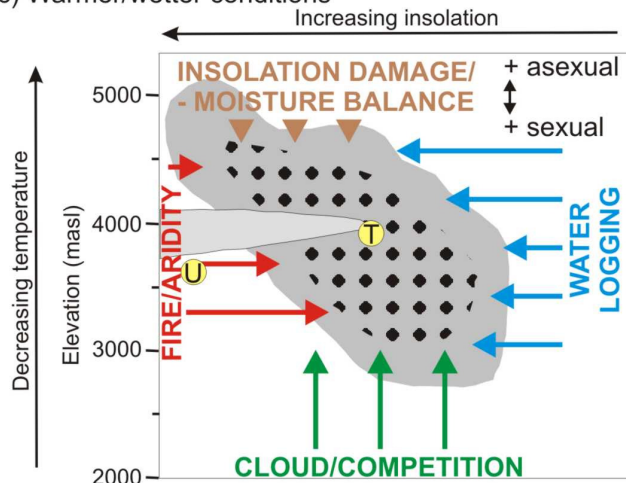


b) Environmental pressures

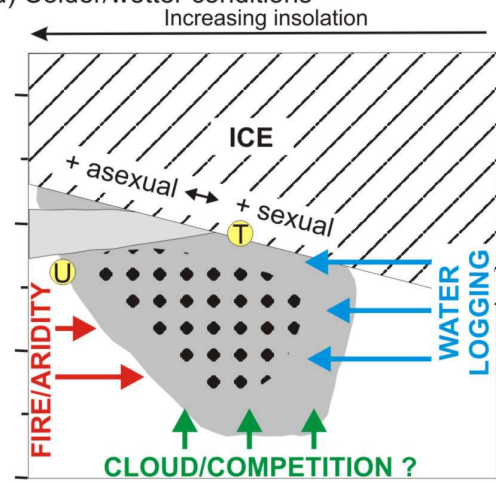


Past climate

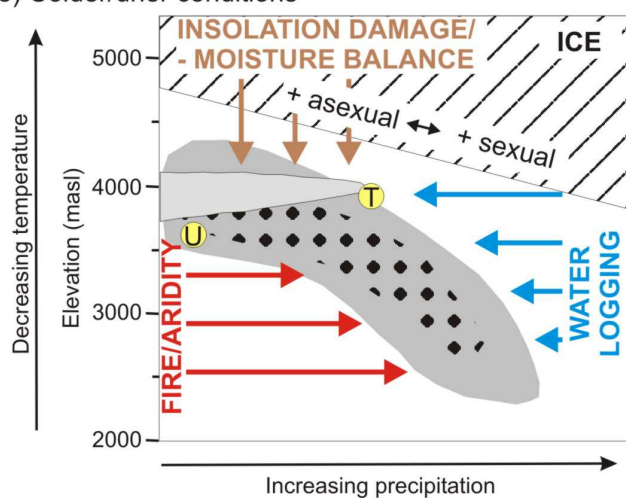
c) Warmer/wetter conditions



d) Colder/wetter conditions



e) Colder/drier conditions



f) Warmer/drier conditions

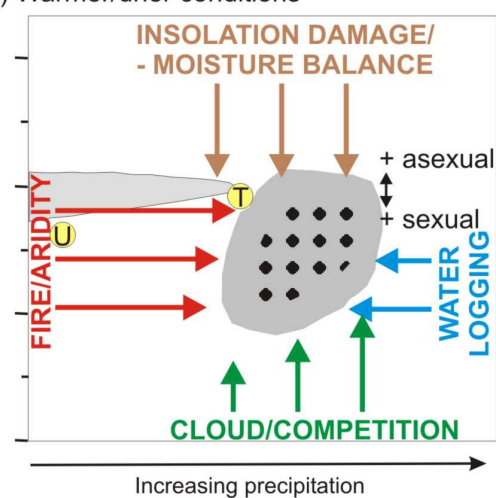
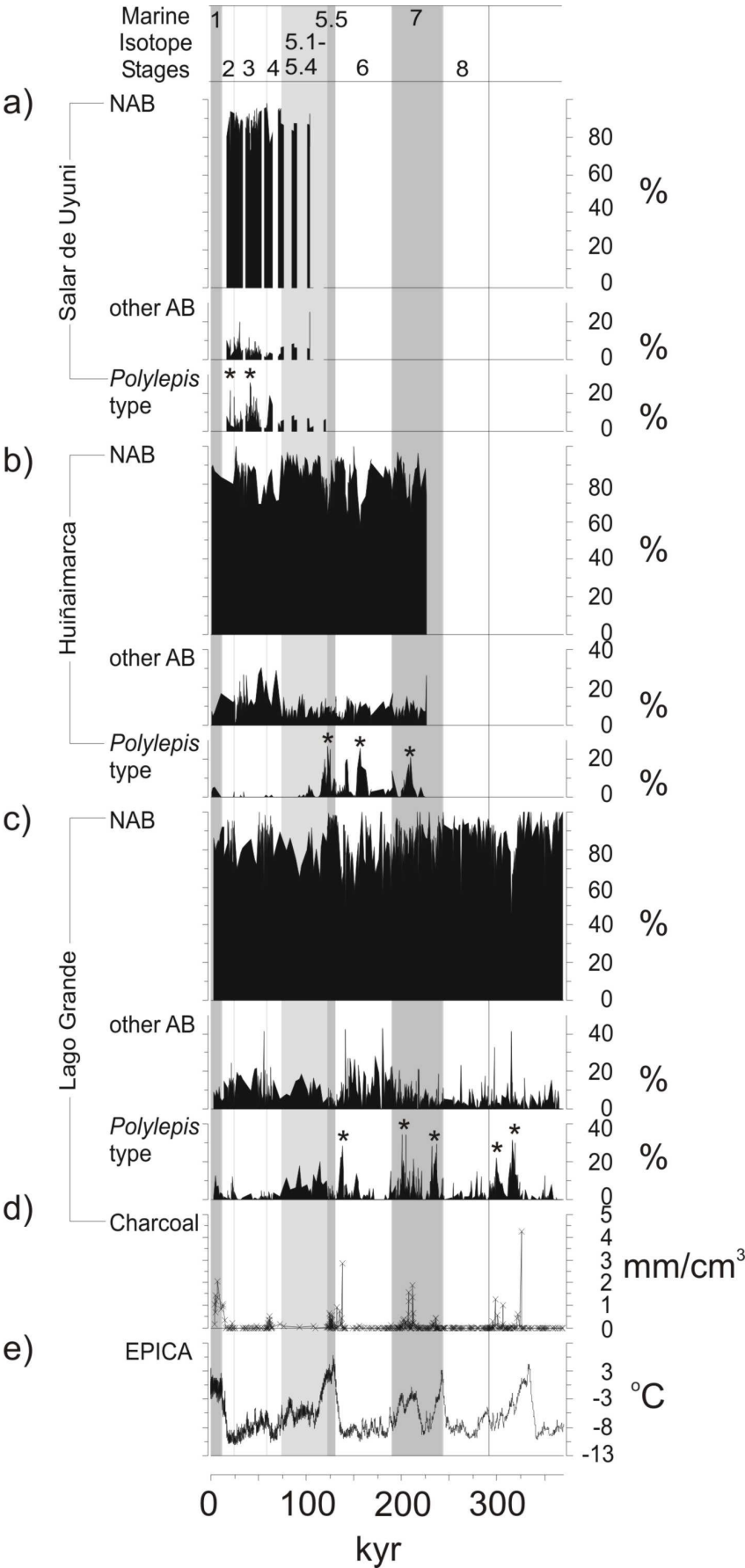


Figure 3



Online supporting information

Table and Figure captions

Table S1. Pollen taxa (>3% in any one sample) included within ‘other tree’ and ‘non-tree’ pollen groups in Fig. 3a-c. Classification follows predominant growth forms for taxon as indicated in Gentry (1993) or Smith et al. (2004).

Fig. S1. Age vs. depth curves for the three study sites: a) Salar de Uyuni (Fritz et al. 2004), b) Huiñaimarca (Tomos 2007), and c) Lago Grande (Hanselman et al. in review).

Table S1

Study site	Other tree taxa	Non-tree taxa
Salar Uyuni	<i>Alnus</i> , <i>Dodonaea</i> , <i>Hedyosmum</i> , Moraceae/Urticaceae, <i>Podocarpus</i> .	Amaranthaceae, <i>Ambrosia</i> , Apiaceae, Asteraceae, Gentianaceae, Poaceae.
Huñaimarca	<i>Acacia</i> type, <i>Alchornea</i> , <i>Alnus</i> , <i>Cecropia</i> , <i>Clethera</i> , <i>Hedyosmum</i> , Melastomataceae/Combretaceae, Moraceae/Urticaceae, <i>Myrica</i> , Myrtaceae, <i>Podocarpus</i> , Rubiaceae, <i>Trema</i> .	<i>Acalypha</i> , Acanthaceae, Amaranthaceae, Apiaceae, Asteraceae, Brassicaceae, Bromeliaceae, Caryophyllaceae, <i>Gunnera</i> , Poaceae, Portulacaceae, Solanaceae, <i>Valeriana</i> .
Lago Grande	<i>Alnus</i> , Anacardiaceae, <i>Clethera</i> , Clusiaceae, Cunoniaceae, Elaeocarpaceae, Euphorbiaceae, <i>Hedyosmum</i> , <i>Juglans</i> , Melastomataceae/Combretaceae, Mimosaceae, Moraceae/Urticaceae, Myricaceae, <i>Podocarpus</i> , Rubiaceae.	<i>Alisma</i> , Amaranthaceae, Apiaceae, Asteraceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Convulvaceae, <i>Ephedra</i> , Ericaceae, Eriocaulaceae, <i>Gentiana</i> , Gerianaceae, <i>Gunnera</i> , Malvaceae, <i>Plantago</i> , Poaceae, Portulacaceae, Ranunculaceae, Scrophulariaceae.

Figure S1

